MIDDLE JURASSIC VEGETATION DYNAMICS BASED ON QUANTITATIVE ANALYSIS OF SPORE/POLLEN ASSEMBLAGES FROM THE RAVENSCAR GROUP, NORTH YORKSHIRE, UK

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Abstract: Quantitative analysis of the distribution of dispersed spores and pollen (sporomorphs) has been used to assess temporal floral variation through the Middle Jurassic Ravenscar Group (Aalenian–Bathonian), North Yorkshire, UK. Aalenian, Bajocian and Bathonian strata possess relatively distinct sporomorph and palynofacies assemblages, which potentially reflect a dynamic history regarding the nature of parent vegetation. Specifically, Aalenian palynofloras are composed of a heterogeneous mixture of conifers, ferns, simple monosulcate pollen producers, sphenophytes and Caytoniales; Bajocian palynofloras are codominated by conifers and ferns; and Bathonian palynofloras are highly rich and contain assemblages of abundant ferns, conifers, lycophytes, pteridosperms/conifers and Caytoniales. Individual- and sample-based rarefaction demonstrates that Bathonian samples are richer than Aalenian and Bajocian samples. Temporal variations in assemblages are a result of long-term depositional and possible climatic fluctuations through the Middle Jurassic. Ordinations of sporomorph data using non-metric multidimensional scaling (NMDS) demonstrate that short-term variations between samples are largely governed by taphonomic biases as a result of slight changes in depositional processes, which give rise to highly variable catchment areas that supply deposits with sporomorphs. Long-term compositional changes are apparent in sporomorph assemblages regardless of lithology/local depositional environments, suggesting that long-term variations are more substantial than short-term variations and potentially include genuine regional temporal changes in parent vegetation. Relating sporomorph assemblages with their respective depositional environments and relative catchment area sizes using lithological and palynofacies information suggests that the basin interior was occupied by mostly low-standing species and extrabasinal vegetation was dominated by coniferous taxa. Comparisons of the dispersed sporomorph and plant megafossil records indicate that both fossil assemblages reflect different aspects of the palaeoflora due to a multitude of taphonomic and ecological biases. Such biases include variation in sporomorph production levels, depositional environment and differential sporomorph and parent plant durability.

Key words: Palynology, sporomorphs, palaeobotany, palynofacies analysis, multivariate analysis, rarefaction analysis.

THE Middle Jurassic deposits of Yorkshire, UK, represent a rare example of an extensive development of predominantly non-marine deposits of this age and therefore provide important insight into understanding terrestrial ecosystems from this time period. The sequences contain abundant and often exceptionally preserved plant megafossil remains and have thus been studied in detail by palaeobotanists over the past century (see Van Konijnenburg-Van Cittert and Morgans 1999). Palaeofloristic reconstructions from these deposits rely primarily on plant megafossil assemblages (e.g. Spicer and Hill 1979), and although several dispersed sporomorph investigations have been carried out (Couper 1958; Chaloner 1968; Chaloner and Muir 1968; Riding and Wright 1989;

Boulter and Windle 1993; Hubbard and Boulter 1997; Srivastava 2011; Slater and Wellman 2015), much of this work has focused on taxonomy and biostratigraphy (Couper 1958; Riding and Wright 1989; Srivastava 2011). This study aimed to build upon previous investigations into the palaeoflora of the Middle Jurassic using sporomorphs (e.g. Boulter and Windle 1993) in an attempt to improve vegetation reconstructions and explain the causes of any potential variations in sporomorph assemblages through time.

Some plant species produce spores/pollen that appear superficially indistinguishable, particularly when only using light microscopy (Frederiksen 1980; Mander and Punyasena 2014). Additionally, linking dispersed spores

and pollen to their parent plants has been hampered by a lack of data on the occurrences of spores and pollen *in situ* within reproductive structures. These two factors represent barriers to reconstructing ancient vegetation using dispersed spores and pollen. However, following extensive investigations over the past half century into the rare occurrences where spores/pollen are preserved *in situ* (e.g. Van Konijnenburg-Van Cittert 1968, 1971, 1978, 1981, 1989, 1993, 2000, 2010; Pedersen *et al.* 1989; Hill 1990; Osborn and Taylor 1993; Balme 1995; Friis and Pedersen 1996; Yang *et al.* 2008) the majority of Middle Jurassic sporomorphs can now be assigned at least to family-level plant classification. In addition, TEM studies of the spore/pollen wall ultrastructure have been used to refine parent plant affinities of dispersed taxa without the need for rare *in situ* preservation (e.g. Batten and Dutta 1997; Slater *et al.* 2015). Thus, dispersed spore/pollen assemblages from the Jurassic of Yorkshire offer important insight into vegetation dynamics of this time period, and, when integrated with the plant megafossil record, these data sets can be used to improve local and regional-scale palaeoenvironmental reconstructions.

GEOLOGICAL SETTING

The geology of the Mesozoic deposits of North Yorkshire (Fig. 1) has been intensively studied since the early nineteenth century (e.g. Young and Bird 1822) as these sequences offer well-exposed, extensive and often highly complex sedimentary successions from this time (e.g. Ielpi and Ghinassi 2014). This study focused on the dominantly non-marine sequences of the Middle Jurassic Ravenscar Group (Aalenian to Bathonian) from the Cleveland Basin (Fig. 2). These successions were deposited at a time of regional uplift and associated sea-level fall. The Ravenscar Group represents predominantly paralic, fluvial and lacustrine deposits, with three marine units that are present as a result of marine incursions from the south and east: the Eller Beck Formation, the Lebberston Member and the Scarborough Formation (Knox 1973; Hemingway and Knox 1973; Livera and Leeder 1981; Alexander 1989, 1992; Powell 2010).

The non-marine Saltwick Formation (Aalenian), at the base of the Ravenscar Group overlies the marine Dogger Formation but often lies unconformably on the Lias Group in areas where the Dogger is absent due to erosion or non-deposition (Powell 2010). The Saltwick Formation mostly consists of channel and crevasse-splay sandstones and floodplain mudstones (Morgans 1999), in which drifted and *in situ* plant megafossils are common (e.g. Spicer and Hill 1979). The Eller Beck Formation represents a thin (*c.* 4 m thick), marine incursion composed of marine sandstone, ooidal ironstone and lime mudstone

(Knox 1973; Hemingway and Knox 1973; Powell 2010). The Cloughton Formation overlies the Eller Beck Formation and represents the thickest formation of the Ravenscar Group (*c.* 85 m). This is divided into three units: the Sycarham Member (non-marine), the Lebberston Member (marine), and the Gristhorpe Member (non-marine). The non-marine units of the Cloughton Formation are predominantly composed of cross-bedded sandstones, siltstones and mudstones throughout which plant beds and thin coal measures are
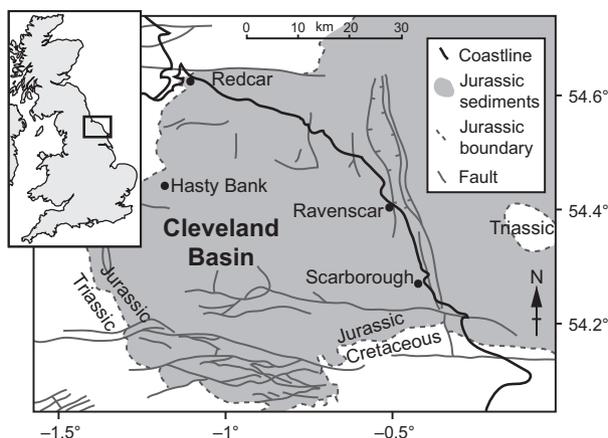
FIG. 1. Generalized geological map of the North Yorkshire coast. Modified from Milsom and Rawson (1989); Mjøs and Prestholm (1993); Palliani and Riding (2000); Rawson and Wright (2000); Slater and Wellman (2015); Slater *et al.* (2015).

FIG. 2. Subdivisions of the Middle Jurassic of Yorkshire, marine units shaded. Modified from Rawson and Wright (2000); Slater and Wellman (2015); Slater *et al.* (2015).

common (Van Konijnenburg-Van Cittert and Morgans 1999). The Lebberston Member is laterally variable and is subdivided into the Millepore Bed and Yons Nab Beds. In coastal exposures the Millepore Bed is composed of a sandy ooidal limestone and calcareous sandstone, whereas inland exposures are more calcareous in composition and referred to as the 'Whitwell Oolite' (Hemingway 1949; Powell 2010). Samples from the Lebberston Member in this study are from coastal outcrops of the Millepore Bed. Overlying the Cloughton Formation, the Scarborough Formation represents the most substantial marine incursion within the Ravenscar Group. Depositional interpretations for the Scarborough Formation include a brackish sandy embayment, a nearshore sandy and muddy shelf and an offshore mud-dominated shelf (Gowland and Riding 1991; Van Konijnenburg-Van Cittert and Morgans 1999). The Scalby Formation is subdivided into the Moor Grit and Long Nab members; this overlies the Scarborough Formation and signifies a return to non-marine, fluviodeltaic conditions (Leeder and Nami 1979; Fisher and Hancock 1985; Riding and Wright 1989). The Moor Grit Member is composed of medium to coarse-grained, cross-bedded channel sandstones; the sequence fines up gradationally into the siltstones, mudstones and fine-grained fluviodeltaic sandstones of the Long Nab Member (Ielpi and Ghinassi 2014).

Although the boundary between the Scarborough and Scalby formations is erosive (Eschard et al. 1991; Powell 2010), the age relationship of these deposits remains unresolved in the literature. One hypothesis suggests that there was no substantial stratigraphic gap between the two formations (Fisher and Hancock 1985; Riding and Wright 1989), whilst the other suggests a considerable time gap spanning the upper part of the Bajocian and lower and middle part of the Bathonian (Leeder and Nami 1979). The latter was supported by Hogg (1993) based on the appearance of certain palynological taxa in the Scalby Formation. However, isotopic analysis of fossil wood across the Scalby–Scarborough Formation boundary provides no evidence for a major stratigraphic gap (Hesselbo et al. 2003) and Rawson and Wright (2000) speculated that the evidence for such a gap is weak.

MATERIAL AND METHOD

Collection

A total of 114 samples were collected through the Ravenscar Group from a combination of coastal outcrop successions and one inland outcrop locality (Fig. 3A). Sampling focused on the following: (1) exposures with fine-grained and reduced sediments likely to yield rich palynomorph assemblages; and (2) non-marine deposits that are known for their plant megafossil contents (i.e. plant beds) to allow comparison between plant megafossil and dispersed sporomorph assemblages. The sampling distribution thus reflects these focus areas. Rock samples represent approximately 1–5 cm in vertical section from individual horizons (i.e. none were composite samples). All sample points and depositional environments for each part of the section are provided in Figures 3–5. Aalenian samples were collected from the Hasty Bank (section 1) (see Spicer and Hill 1979; Slater and Wellman 2015) and Hayburn Wyke (section 2) plant beds (discussed in Van Konijnenburg-Van Cittert and Morgans 1999). Bajocian samples were collected from Cloughton Wyke (section 3), Cayton Bay and Yons Nab (section 4). A number of samples from Cloughton Wyke were collected and analysed by Cadman (1979), the slides have been reassessed here to ensure taxonomic consistency. Bathonian samples were collected from sections at Burniston Bay (section 5), through which dinosaur footprints are common (Rawson and Wright 2000). Twelve coal samples were collected; these originate from thin, laterally discontinuous deposits (typically <10 m in lateral section). Soft clay horizons that contained rootlets were present beneath the coals at Hayburn Wyke and Cloughton Wyke.

Processing

Dry rock samples were weighed at 20 g before being dissolved in 40% hydrochloric acid for at least 24 hours to remove carbonates, followed by two-week maceration in 40% hydrofluoric acid to remove silicates. Samples were agitated every two days to ensure full break down of rock material. Excess liquid was then decanted and fresh water added, repeating the process until neutral before sieving at 10 or 20 μm; no sporomorphs were found less than 20 μm in diameter in samples that were sieved at 10 μm; thus, it was deemed adequate to sieve further samples at 20 μm. One day was left between decants to ensure minimal loss of palynomorphs. Centrifuging residues in zinc chloride was then undertaken to remove heavy minerals. Residues were then sieved again at 10 or 20 μm to remove the heavy liquid and final residues were spread across cover slips and gently heated on a hot plate to remove excess water. Cover slips were then mounted onto slides using epoxy resin on a hot plate. Five of the 12 coal samples were processed using Schulze solution overnight, before being neutralized with water and sieved at 20 μm. The remainder of the processing method followed the same procedure as all other samples. A number of excess residues were sieved at 100 μm for megaspores and larger floral components. Specimens were picked
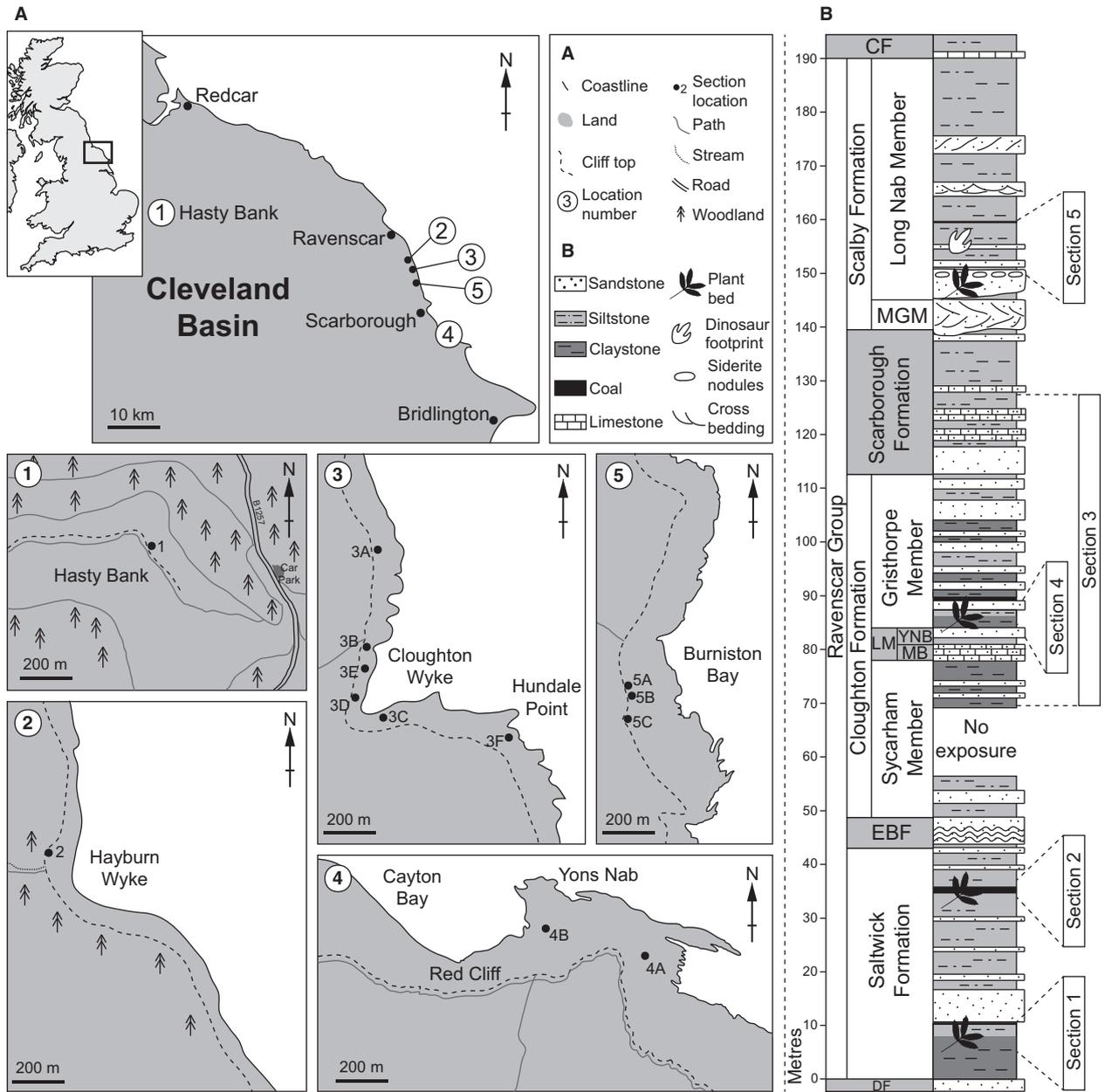
FIG. 3. Localities and sampling points through the Middle Jurassic of Yorkshire. A, locations of all sections with detailed maps of individual section locations. B, composite sedimentary log of the Middle Jurassic of Yorkshire with the stratigraphic positions of sections 1–5. Shaded text regions represent marine units; CF, Cornbrash Formation; DF, Dogger Formation; EBF, Eller Beck Formation; LM, Lebberston Member; MB, Millepore Bed; MGM, Moor Grit Member; YNB, Yons Nab Beds. Maps 1, 2 and 4 modified from Van Konijnenburg-Van Cittert and Morgans (1999).

using a fine paint brush and mounted on SEM stubs, gold coated using an Edwards Coater 5250B for 3 min, and examined under a Philips XL20 field emission SEM at 15 kV. Processing details for all samples are provided in Slater and Wellman (2016, appendix S1). All materials (rock samples and slides) are housed in the collections of the Centre for Palynology at the University of Sheffield, UK.

Counting

Slides were examined under a Meiji Techno (MA151/35/50) light microscope. A minimum of 200 sporomorphs were counted from each sample. Counts were carried out in systematic traverses to ensure no grains were missed. The remainder of the slide was then examined in the same fashion to identify rare species that were not present
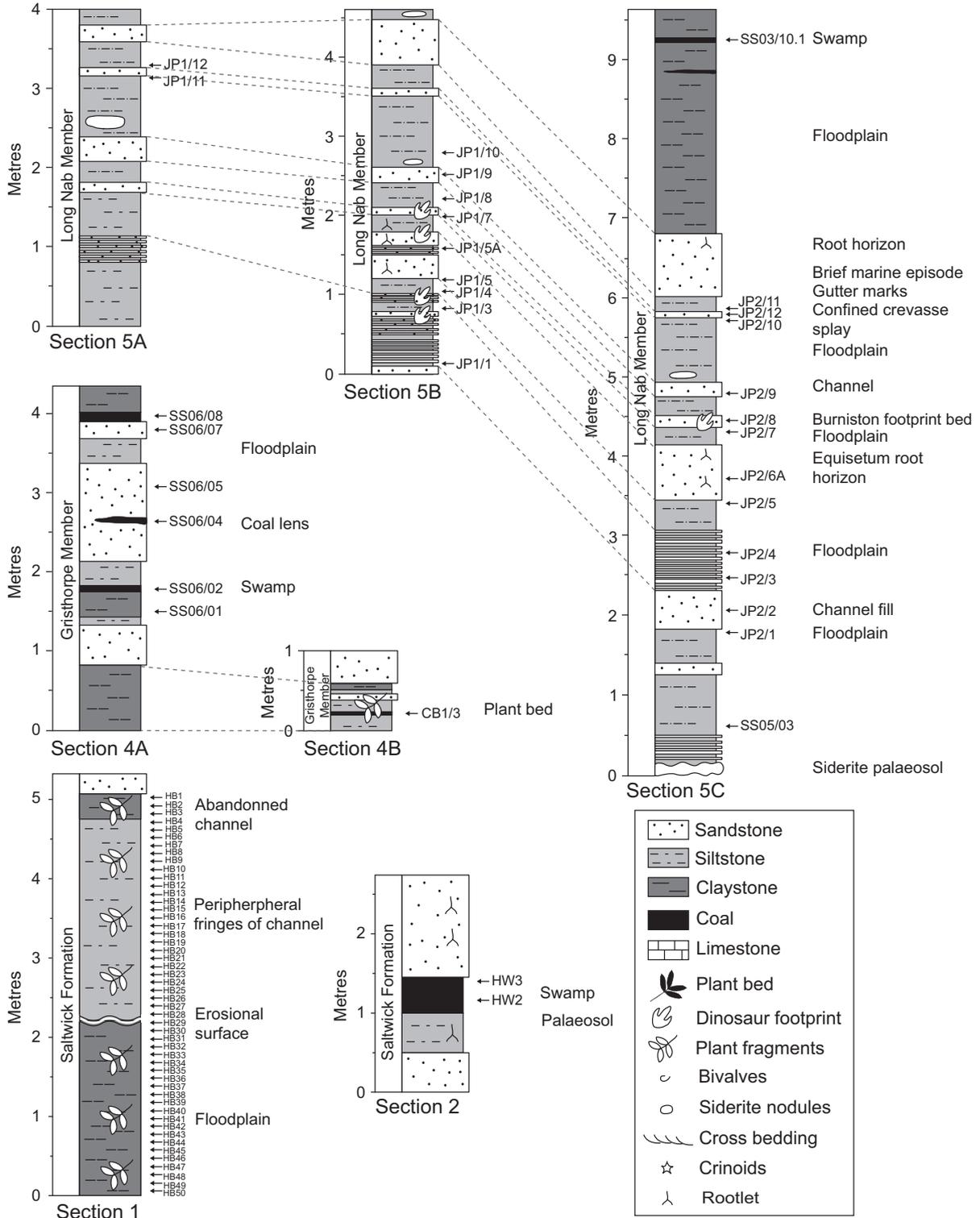
FIG. 4. Detailed sedimentary logs of sections 1, 2, 4 and 5 with sample points and palaeoenvironmental interpretations.

in the count data. The complete sporomorph raw data set is provided in Slater and Wellman (2016, appendix S2). Selected taxa are shown in Figure 6, for further sporo-

morph images that refer closely to the taxonomic identifications used in this study see Couper (1958), Boulter and Windle (1993) and Srivastava (2011).
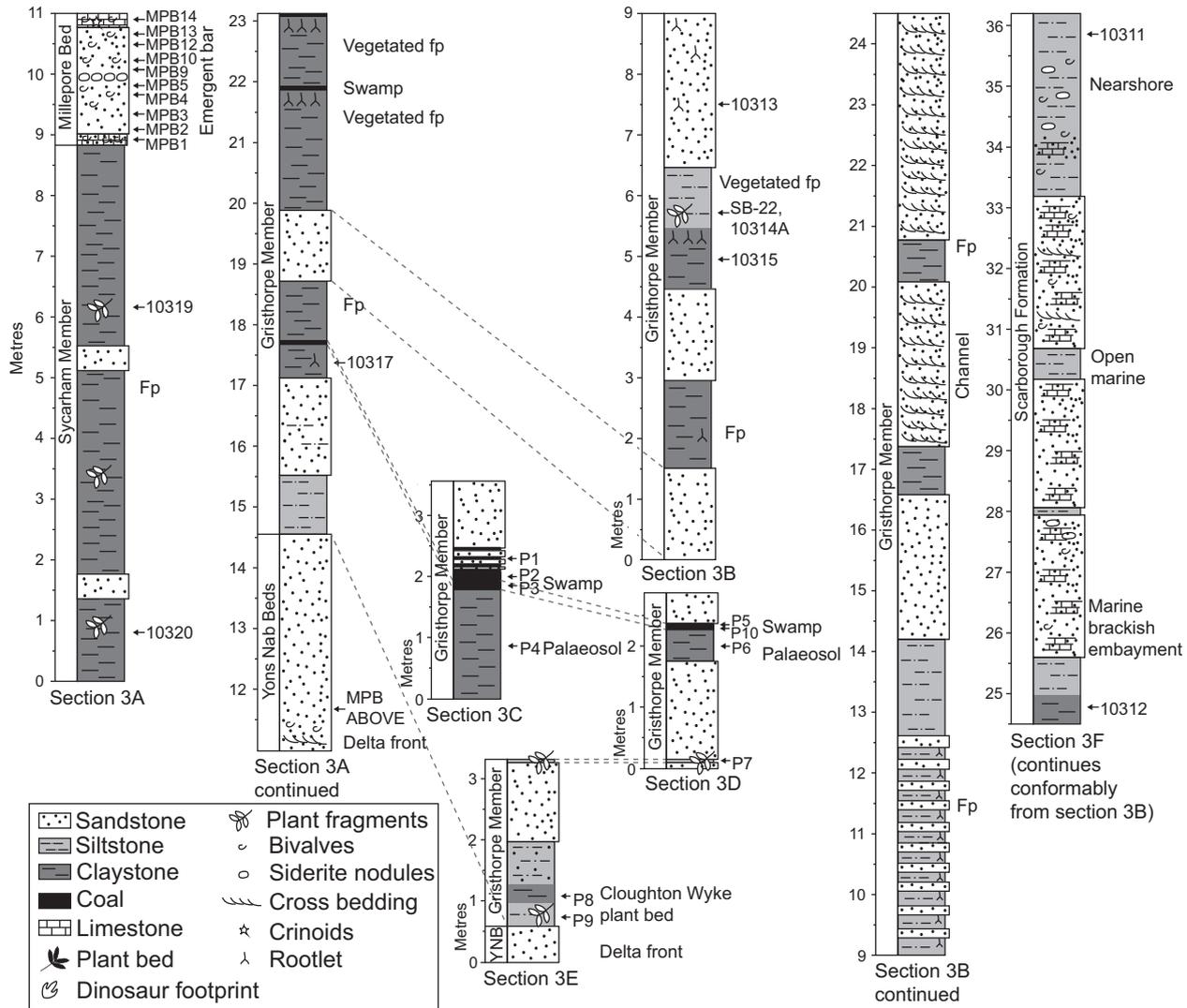
FIG. 5. Detailed sedimentary logs of section 3 with sample points and palaeoenvironmental interpretations. Fp and fp, floodplain; YNB, Yons Nab Beds.

Palynofacies analysis

Basic palynofacies analysis was undertaken on all samples to assess differences in depositional environments between samples. The term palynofacies typically refers to all of the visible organic particles (usually between 2 and 250 μm in size) that occur within palynological maceration residues

(Traverse 2007). Palynofacies analysis is commonly used to assess depositional environments (e.g. Parry *et al.* 1981; Boulter and Riddick 1986; Van der Zwan 1990; Brugman *et al.* 1994; Oboh-Ikuenobe and Yepes 1997; Oboh-Ikuenobe *et al.* 2005; Carvalho *et al.* 2006). Categories for palynofacies debris are as follows: spores, pollen, algae, dinoflagellate cysts, acritarchs, humic debris, amorphous

FIG. 6. Selected sporomorphs from the Ravenscar Group. Note that the dispersed spores are extremely well preserved and of low thermal maturity (translucent and pale yellow in colour). A, *Densoisporites velatus*, sample JP2/11ii (England finder V44/3). B, *Matonisporites phlebopteroides*, sample SS06/04i (England finder U39/2). C, *Cibotiumspora jurienensis*, sample JP2/8ii (England finder F43/C). D, *Deltoidospora minor*, sample JP2/6Aii (England finder H31/4). E, *Vitreisporites pallidus*, sample HB8i (England finder O32/2). F, *Perinopollenites elatoides*, sample JP1/3ii (England finder L22/3). G, *Eucommiidites troedssonii*, sample HB9i (England finder O29/C). H, *Paxillitriletes phyllicus* (megaspore), sample JP2/3i (England finder U35/4). I, *Paxillitriletes phyllicus* (megaspore), sample JP2/3 (SEM stub SS10). A–H, light microscope images; I, SEM image. A–G, scale bar represents 20 μm; H–I, scale bar represents 100 μm. Colour online.

organic matter (AOM), *Botryococcus*, structured vitrinite, unstructured vitrinite, cuticle and inertinite. For comprehensive descriptions and figures of palynofacies categories, see Tyson (1995) and Batten and Stead (2005). In the classification scheme used here 'spores' refers to trilete spores; 'pollen' refers to all pollen morphotypes; 'algae' refers to all
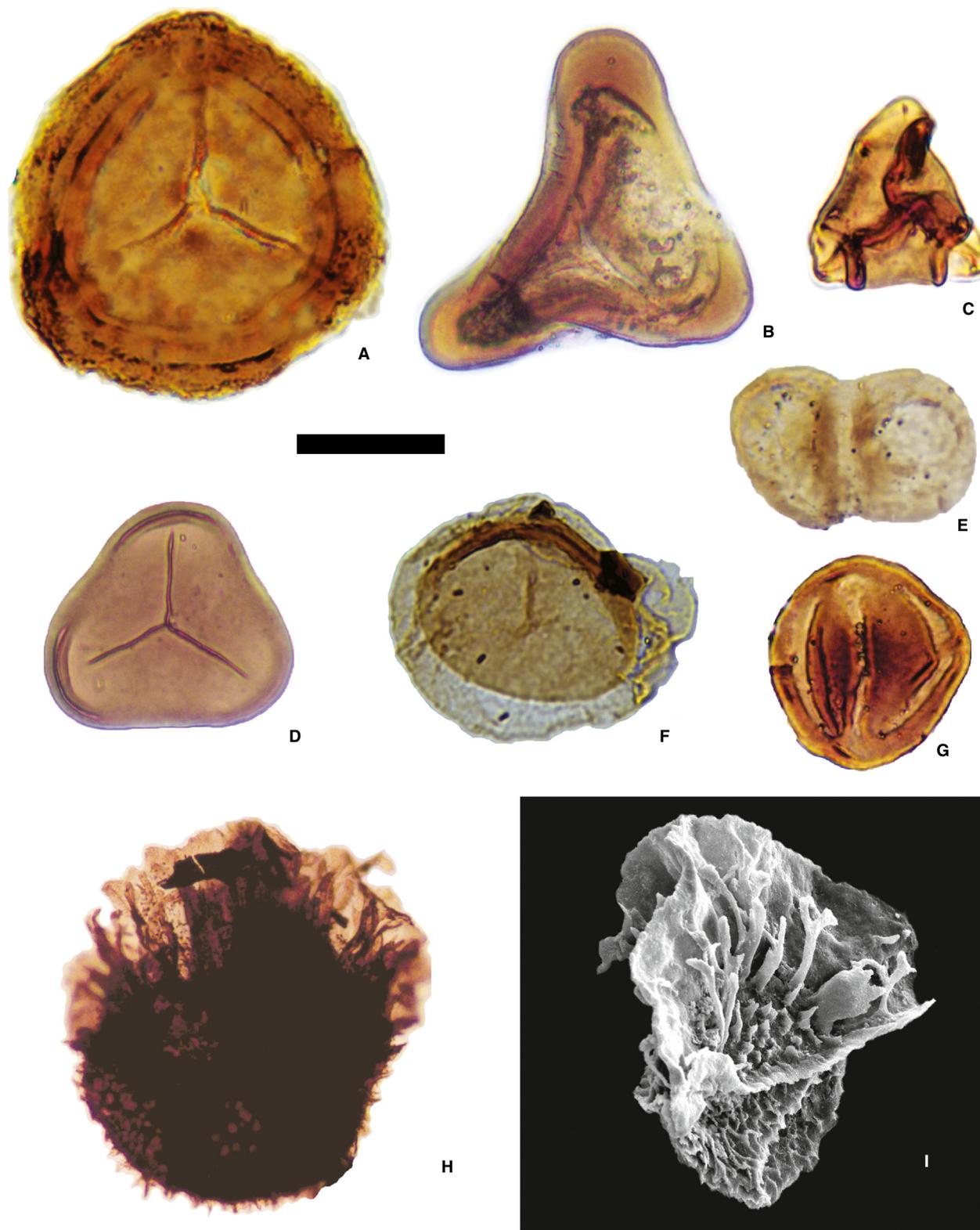
algal forms that are not *Botryococcus*; 'dinoflagellate cysts' and 'acritarchs' represent marine palynomorphs which belong to these groups; 'humic debris' refers to yellow–brown humic material exhibiting little structure; 'AOM' refers to unstructured, amorphous organic matter; '*Botryococcus*' represent fresh/brackish water algal colonies; 'structured vitrinite' refers to translucent–brown, lath-shaped to blocky woody particles that exhibit longitudinal structural thickenings; 'unstructured vitrinite' refers to brown woody material that has undergone extensive degradation; 'cuticle' refers to transparent to yellow epidermal fragments; and 'inertinite' refers to black woody material. Counts of 200 palynodebris particles were carried out on all samples, the complete palynofacies raw data set is provided in Slater and Wellman (2016, appendix S3).

Data analysis

Individual- and sample-based rarefaction analyses were undertaken to assess changes in richness through the sequence. Individual-based rarefaction calculates the expected richness of a sample at a lower count total so that different count sizes can be compared more fairly (e.g. Gotelli and Colwell 2001). Sample-based rarefaction is used on groups of samples to calculate the expected richness at lower numbers of pooled samples (e.g. Jardine and Harrington 2008). Individual-based rarefaction curves were calculated for each sample and plotted for each stage to compare richness between stages. Count data was also rarefied at 200 specimens per sample to construct a rarefied richness plot through the sequence. A problem with individual-based rarefaction is that when a small number of taxa are highly abundant, as is the case in many samples here, a large portion of the richness data (taxa that are present in slides but not in counts) is excluded from the analysis. Thus, raw richness data is also provided as this includes all taxa that were present in each sample. Richness patterns present in both raw and rarefied plots are therefore potentially more reliable. Sample-based rarefaction, using presence–absence data was also carried out on grouped samples from the Aalenian, Bajocian and Bathonian to assess broad changes in richness between stages. Rarefaction analysis was carried out using PAST (Hammer *et al.* 2001).

The ordination technique non-metric multidimensional scaling (NMDS) was used to assess compositional change between sporomorph samples. NMDS is a non-parametric ordination method that uses ranked distances between samples to assess the degree of similarity between samples. This enables complex multivariate data to be plotted onto a minimal number of axes (e.g. Jardine *et al.* 2012). In NMDS ordinations, samples that are compositionally similar plot close together, whereas samples that are compositionally dissimilar plot far apart. The Bray–Curtis dissimilarity metric was used to generate distances between samples as this method is considered to perform well in ecological studies (e.g. Harrington 2008). Repeated runs were carried out for two dimensions until a convergent solution was established. Principal components rotation and centring was then carried out to the final ordination. NMDS was carried out using R, version 3.1.2 (R Core Team 2014), within the package vegan, version 2.2–1 (Oksanen *et al.* 2015). Ordinations displayed here were performed on sporomorph relative abundance and presence–absence data sets (e.g. Harrington 2008). Unlike ordination of relative abundance data, which can be strongly controlled by the most abundant taxa, ordination of presence–absence data is not affected by this problem, as all taxa within a sample are equally weighted in the ordination. For the relative abundance data matrix, species that were present in samples but not in counts and singletons in the count data (samples present in one sample) were removed from the data set to reduce statistical noise. For the presence–absence matrix all taxa were included; taxa that were present were scored as '1' and taxa that were absent were scored as '0'. NMDS ordinations were also carried out on sporomorph data sets following logarithmically transforming relative abundances (e.g. Slater and Wellman 2015) and the Wisconsin double-standardization method (e.g. Jardine and Harrington 2008; Mander *et al.* 2010). The ordinations and stress values from these plots are highly similar to the unaltered relative abundance NMDS plot; thus, it was deemed unnecessary to manipulate abundances and so unaltered relative abundances are presented here. The high degree of similarity between NMDS plots using different data manipulation techniques demonstrates that the results are robust.

RESULTS

Temporal sporomorph variation and vegetation reconstruction

A total of 85 sporomorph taxa were identified from 114 palynological samples; the entire taxonomic list with proposed botanical affinities is provided in Slater and Wellman (2016, appendix S4). These associations are mostly based on the relatively rare situations where spores/pollen are preserved *in situ* (e.g. Van Konijnenburg-Van Cittert 1981). Figure 7 displays an example of *in situ* spores from a fern sporangium recovered from sample JP2/2. The spores are smooth walled and trilete; however, assigning these to a genus with confidence is difficult due to their orientation and lack of obvious defining features.

The commonly used Chao2 species richness estimator, with bias correction (e.g. Gotelli and Colwell 2011) gave a species estimate of 91.94 taxa (standard deviation = 7.07) for the entire data set, which suggests the data was not

FIG. 7. Fern sporangium with *in situ* spores, from sample JP2/2. A, overview of sporangium. B, close-up of A showing smooth walled spores within sporangium. C, close-up of A showing smooth walled spore with probable trilete mark. All scale bars represent 25 μm.
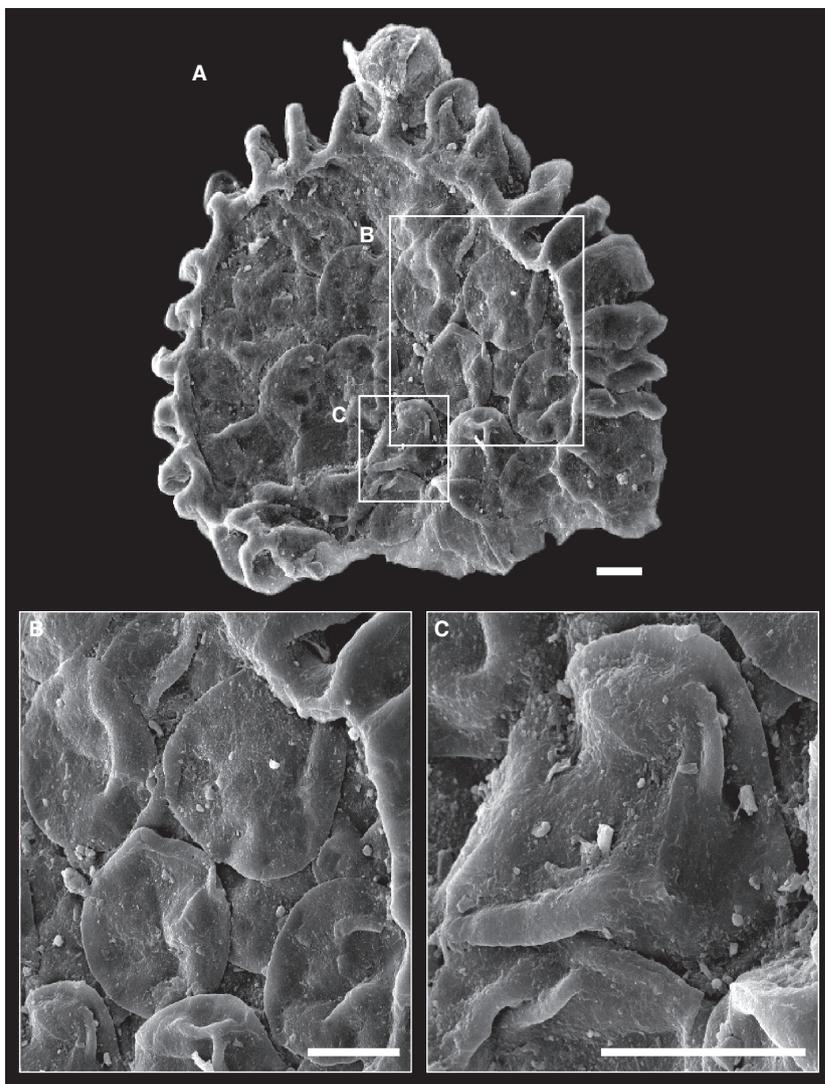
severely undersampled. Relative abundances of the ten most abundant species are provided in Figure 8A, with richness data for every sample provided in Figure 8B–C. Sporomorphs have been grouped into their respective botanical affinities in Figure 9 to assess large-scale vegetation change through the Ravenscar Group. Figures 8–9 reveal that the Aalenian, Bajocian and Bathonian samples have relatively distinct sporomorph assemblages regarding the overall abundances of certain species and plant groups. Section 4 and the lower part of the Gristhorpe Member in section 3 are roughly synchronous; however, it is difficult to correlate samples from these sections with certainty; thus, section 4 has been excluded from the composite sporomorph abundance/richness plots and is shown below them (Figs 8–9, 13).

Regarding sporomorph groupings, the 'Monosulcate producers' group (Fig. 9) refers to simple monosulcate pollen of the genera *Chasmatosporites* and *Cycadopites*.

Chasmatosporites is known to have botanical affinities within the Cycadales and Ginkgoales and *Cycadopites* has broad botanical affinities within the Cycadales, Ginkgoales, Peltaspermales and Bennettitales (e.g. Townrow 1960; Balme 1995; Mander 2011). Plant megafossil studies (e.g. Spicer and Hill 1979) demonstrate that Cycadales, Ginkgoales and Bennettitales are common from the Yorkshire Jurassic; thus, these sporomorphs probably originate from a mixture of these groups. The 'Pteridosperms/Conifers' group (Fig. 9) refers to species of *Alisporites*. These are considered to have both pteridosperm and/or coniferous origins (Mander 2011).

Aalenian. Sporomorph assemblages from the lower Saltwick Formation at Hasty Bank (section 1) contain abundant *Araucariacites australis*, *Calamospora mesozoica*, *Classopollis torosus*, *Dictyophyllidites harrisii* and *Perinopollenites elatoides* with higher abundances of *Cycadopites*,
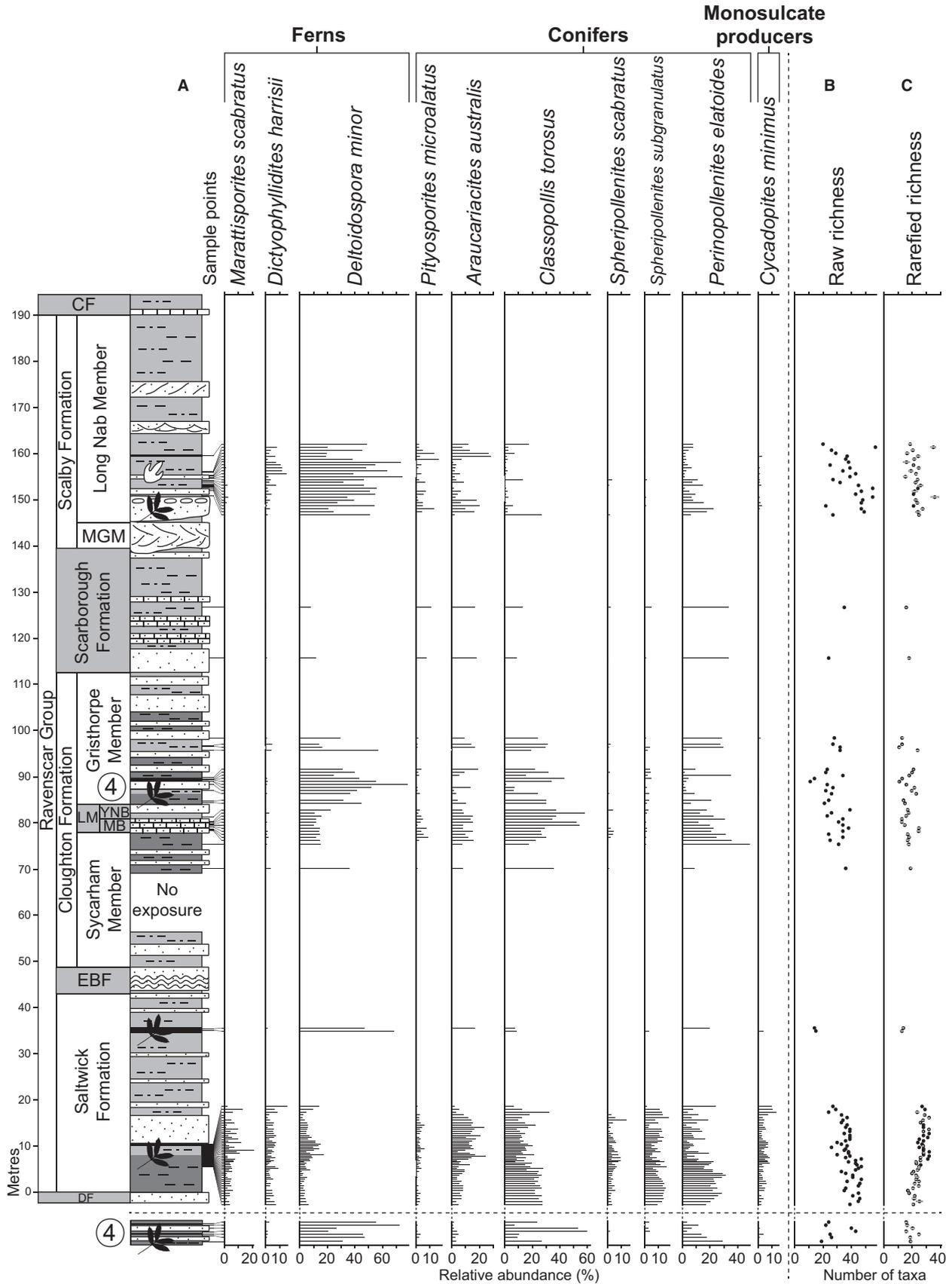
Marattisporites scabratus and *Spheripollenites* and lower abundances of *Deltoidospora minor* compared to the rest of the section (Fig. 8A). Assemblages from the lower part of section 1 (claystone) differ from the upper part (siltstone and grey clay) in that abundances of *Callialasporites turbatus*, *C. torosus* and *P. elatoides* are higher and abundances of *A. australis* and *Deltoidospora* are lower in the claystone. Assemblages from the coal samples of section 2 contain abundant *D. minor* with low abundances of all other taxa.

In general, Aalenian samples are co-dominated by conifers and ferns (conifers are more abundant than ferns) and have considerably more simple monosulcate and sphenophyte sporomorphs with moderately more Caytoniales and Erdtmanithecales pollen compared to Bajocian and Bathonian samples (Fig. 9). Fern spores are considerably less abundant within Hasty Bank samples compared to the Bajocian and Bathonian counterparts. The low abundances of *M. scabratus* (Fig. 8A) demonstrate that Marattiaceae ferns contrast the general abundance pattern of the ferns through the Ravenscar Group and are abundant within the Aalenian, but become considerably less abundant in the Bajocian and Bathonian. Abundant *C. mesozoica* suggests that sphenophytes were more common in the Aalenian compared to the Bajocian and Bathonian (Fig. 9).

Bajocian. Assemblages from the Sycarham Member contain abundant *C. torosus*, *D. minor* and *P. elatoides* (Fig. 8A) with generally low abundances of all other taxa. Assemblages from the Lebberston Member possess abundant *C. torosus* and *P. elatoides* with moderate abundances of *A. australis* and low abundances of *D. minor* (Fig. 8A). The Gristhorpe Member contains abundant *C. torosus* and *D. minor* with moderately abundant *A. australis* and relatively low abundances of *P. elatoides* in the lower samples of the Gristhorpe Member, which increases in abundance within samples from the middle part of the Gristhorpe Member (Fig. 8A). Assemblages from the Scarborough Formation are predominantly composed of abundant *A. australis*, *Cerebropollenites mesozoicus*, *P. elatoides*, *Pityosporites microalatus* and low abundances of *C. torosus* and *D. minor* (Fig. 8A).

Bajocian palynofloras are unsurprisingly intermediate in terms of plant group abundances (Fig. 9) between the Aalenian and Bathonian assemblages. Similarly to the Aalenian samples, conifers dominate abundances and lycophytes and pteridosperms/conifers are low in abundance. However, unlike the Aalenian assemblages, fern spores are considerably more abundant in the Bajocian and monosulcate producers and sphenophytes are notably less abundant in the Bajocian (Fig. 9).

Bathonian. Assemblages of the Long Nab Member are composed of abundant *Alisporites*, *A. australis*, *D. minor*, *Dictyophyllidites harrisii* and *P. microalatus* with low abundances of *C. torosus* and *P. elatoides* (Fig. 8A). In contrast to the Aalenian and Bajocian assemblages, conifer pollen is less abundant than fern spores in the Bathonian (Fig. 9). In particular, abundances of Cheirolepidiaceae pollen (*C. torosus*) and Taxodiaceae pollen (*P. elatoides*, *Spheripollenites scabratus* and *Spheripollenites subgranulatus*) are considerably lower in Bathonian samples compared to Bajocian and Aalenian samples (Fig. 8A). The large trees of the Cheirolepidiaceae are typical of dry floodplain environments, whereas the Taxodiaceae trees are typical of swamp/poorly drained floodplain environments (Stukins *et al.* 2013). A reduction in both plant groups, which reflect quite different environmental conditions suggests perhaps: (1) an increased dominance of low-standing vegetation types, including ferns and lycophytes over large, coniferous varieties; and/or (2) a reduction in geographical catchment area from which sporomorphs are being supplied from, perhaps due to depositional change. Similarly to the Bajocian palynofloras, abundances of monosulcate producers and sphenophytes remain low into the Bathonian (Fig. 9). However, abundances of lycophytes and pteridosperms/ conifers increase markedly in the Bathonian from the Bajocian and Aalenian (Fig. 9).

Several of the major temporal abundance changes seen here agree with the findings of Couper (1958). Specifically, *C. torosus* and *C. mesozoica* are more abundant in the Saltwick (Lower Deltaic Series in Couper 1958) and Cloughton (Middle Deltaic Series in Couper 1958) formations compared to the Scalby Formation (Upper Deltaic Series in Couper 1958); *D. minor* (*Cyathidites minor* in Couper 1958) is notably less abundant in the Saltwick Formation compared to the Cloughton and Scalby formations; and *P. microalatus* (*Abietineaepollenites microalatus* in Couper 1958) is more abundant in the Scalby Formation. The major abundance changes recognized in Figures 8A and 9 loosely correlate with the Aalenian, Bajocian and Bathonian boundaries respectively. The timing of these changes potentially indicates the following: (1) extensive floral

FIG. 8. Sporomorph abundance and richness charts. Shaded text regions in the log represent marine units; CF, Cornbrash Formation; DF, Dogger Formation; EBF, Eller Beck Formation; LM, Lebberston Member; MB, Millepore Bed; MGM, Moor Grit Member; YNB, Yons Nab Beds. A, relative abundances of the ten most abundant sporomorph taxa. B, raw richness for all samples. C, rarefied richness (at 200 specimens) for all samples, horizontal bars across sample points represent 95% confidence intervals. In the composite log '4' refers to the stratigraphic position of section 4.
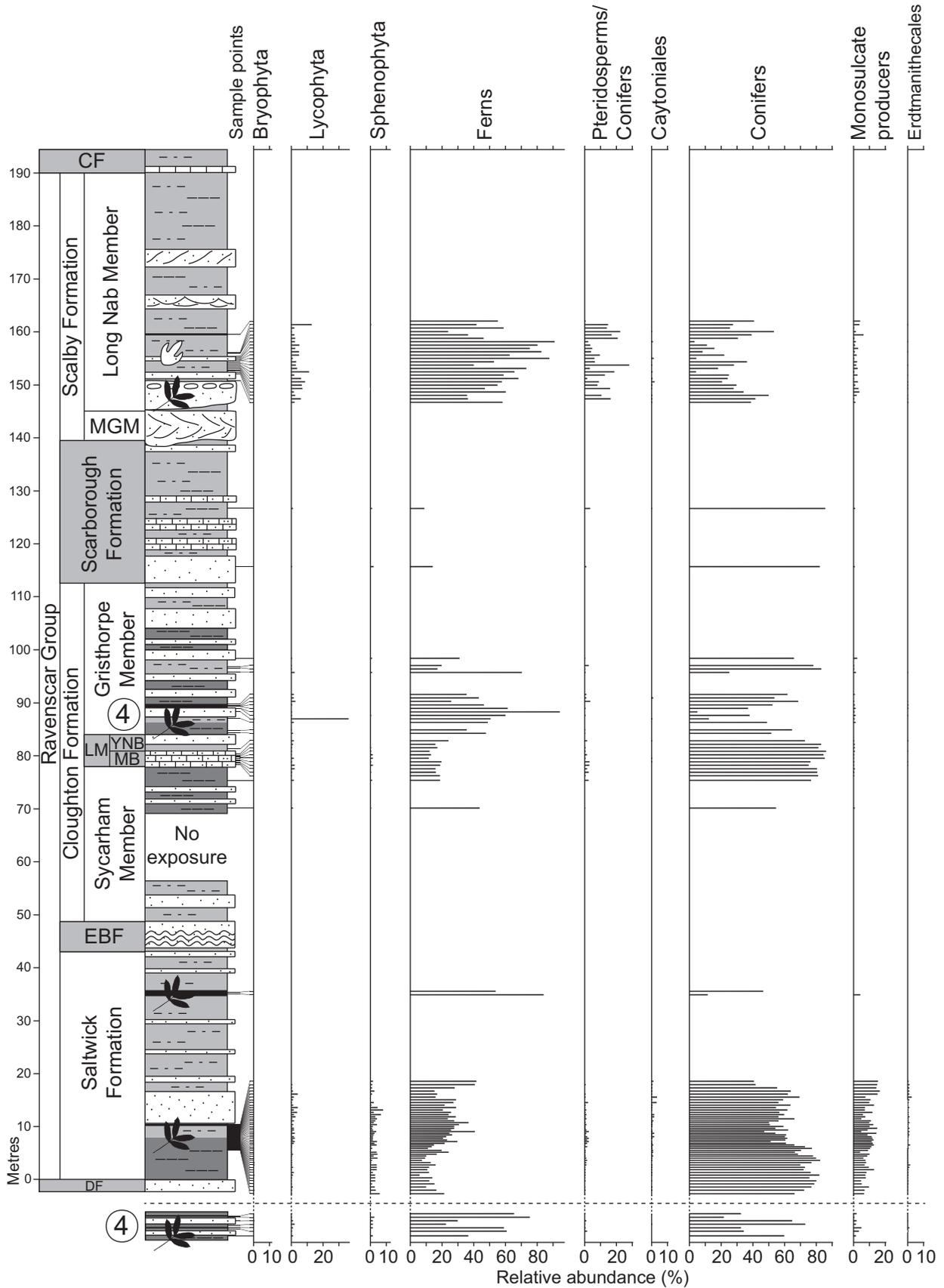
turnover between these three stages; and/or (2) substantial changes in taphonomic biases to preserve quite different sporomorph assemblages between stages.

Richness changes

Similarly to abundance patterns, richness data appears to vary distinctly between the Aalenian, Bajocian and Bathonian stages. Raw richness for every sample (Fig. 8B) is moderately high in the Aalenian and decreases into the Bajocian, raw richness then increases to its highest levels in the Bathonian. When counts are rarefied at 200 specimens (Fig. 8C), broad temporal patterns are similar to the raw richness changes. Rarefied richness is high in the Aalenian, and this decreases into the Bajocian and then increases to its highest levels in the Bathonian. Individual-based rarefaction curves for all samples (Fig. 10) agree with the overall raw and rarefied richness patterns seen in Figure 8B–C, although the curves reveal that there is substantial overlap between samples of different stages. Figure 10 suggests that Aalenian samples are typically richer than Bajocian samples and Bathonian samples display extensive variation, but possess the two richest samples (JP1/3 and JP2/11). Interestingly, in the Hasty Bank plant bed (section 1) raw and rarefied richness data in Figure 8B–C display conflicting temporal records. Specifically, raw richness is consistently higher in the lower part of the section compared to the upper part, but the opposite pattern is recorded by the rarefied richness data. This highlights a weakness when rarefying counts; samples from the lower part of the section contain higher abundances of conifer pollen, in particular *Classopollis* and *Perinopollenites*; thus, rarefied values are 'artificially' reduced due to the high conifer abundances as a substantial portion of the richness data is not contained within the count data. The raw richness values are therefore almost certainly more representative of 'true' richness changes in this part of the section.

Coal samples often display low richness levels within individual-based rarefaction plots (Fig. 10). For example, the Aalenian Hayburn Wyke coals are markedly less rich than all other Aalenian samples. This potentially reflects the probable small representative source areas for these deposits. Some coals however display relatively high richness levels (e.g. SS06/02 in the Bajocian). The variation in richness levels between coals suggests that the source areas and potentially time periods represented by these samples varied between deposits, hence the depositional settings and formation processes may have varied.

Sample-based rarefaction (Fig. 11) demonstrates that Bathonian samples are richer than Aalenian and Bajocian samples and, unlike individual-based rarefaction, suggests that richness between Aalenian and Bajocian samples is very similar. Sample-based rarefaction is potentially a more reliable method than individual-based rarefaction here as sample-based rarefaction includes all species that are present in each slide; therefore, the method is not affected by highly abundant taxa, as is the case with individual-based rarefaction. However, the results may indicate that the same species are reoccurring in the Aalenian samples and thus with additional samples, sample-based rarefaction curves do not display a large increase in richness. Conversely, in the Bajocian samples the among-sample richness may be higher even though within-sample richness is lower. For example, different taxa may be present within different samples, even though the total number of taxa within each sample may be low; thus with additional samples, sample-based rarefaction curves appear markedly richer than individual-based rarefaction curves.

Sample ordination

NMDS of relative abundance data (Fig. 12A) and presence–absence data (Fig. 12B) reveals that samples from the Aalenian, Bajocian and Bathonian stages are well separated in ordination space, with only minimal overlap. This demonstrates a clear change in sporomorph assemblage composition through time and, similarly to abundance and richness plots (Figs 8–11), suggests that the Aalenian, Bajocian and Bathonian stages possessed relatively distinct floras, both in terms of species abundances and the presence/absence of taxa. It should be noted that the presence–absence NMDS shows a less clear separation of stages than the relative abundance NMDS. This suggests that the relative abundance shifts in range through taxa are more important than differences in composition (i.e. which taxa are present or absent) among the three stages. In both ordinations (Fig. 12) samples primarily cluster according to their age, regardless of lithology, indicating that the stratigraphic position of a sample is more important than its lithology/local depositional environment through the Ravenscar Group. However, there are groupings of similar lithologies, and coal samples are more scattered across plots; this potentially reflects the generally low richness of coals due to their probable small representative source arees. Thus, composition varies to a

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FIG. 9. Relative abundances of sporomorphs grouped into their respective affinities. Shaded text regions in the log represent marine units; CF, Cornbrash Formation; DF, Dogger Formation; EBF, Eller Beck Formation; LM, Lebberston Member; MB, Millepore Bed; MGM, Moor Grit Member; YNB, Yons Nab Beds. In the composite log '4' refers to the stratigraphic position of section 4.
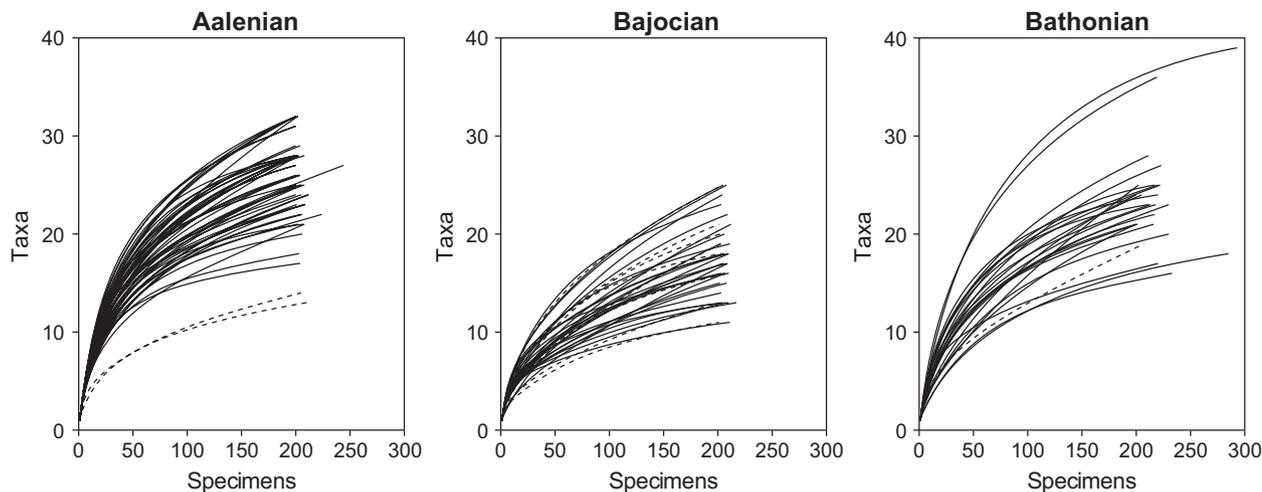
FIG. 10. Individual-based rarefaction curves for all samples separated into the Aalenian, Bajocian and Bathonian stages. Dashed lines represent coal samples. The 95% confidence interval lines have been removed for clarity.
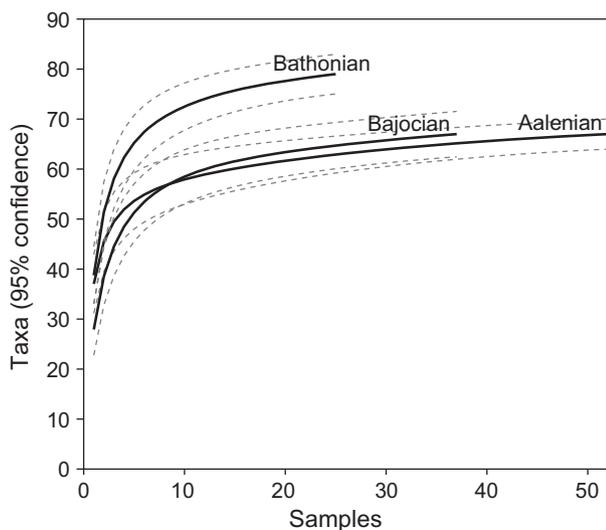
FIG. 11. Sample-based rarefaction curves for Aalenian, Bajocian and Bathonian samples. Dashed grey lines represent 95% confidence intervals.

measurable degree regarding the lithology of a sample, which potentially reflects different vegetation and/or different depositional processes to preserve different assemblages. This is however secondary to the temporal position of a sample, which, with the exception of coals, is evident in ordinations regardless of lithology. Axis scores for Figure 12 are provided in Slater and Wellman (2016, appendices S5 and S6).

Palynofacies analysis

Abundances of organic debris are provided in Figure 13. Most samples are composed of a heterogeneous mixture of organic debris, co-dominated by AOM, inertinite, unstructured vitrinite, pollen and spores. Abundant AOM throughout the Ravenscar Group suggests relatively low oxygen and high nutrient levels within the original water during deposition (Tyson 1995; Roncaglia 2004; Traverse 2007; Pacton *et al.* 2011). Similarly to sporomorph assemblages, stratigraphic variation is visible in palynofacies assemblages between the Aalenian, Bajocian and Bathonian stages, which potentially reflects long-term depositional and/or vegetation change through time. Short-term variations in assemblages are also present between stratigraphically adjacent samples from individual sections, which roughly correlate with lithological variation. Aalenian samples are composed of high abundances of inertinite, structured vitrinite and low abundances of spores compared to Bajocian and Bathonian samples. Bajocian samples contain considerably more spores, slightly more cuticle and less structured vitrinite and inertinite compared to Aalenian samples, and Bathonian samples contain high abundances of cuticle and spores compared to Aalenian and Bajocian samples. Unsurprisingly, samples from the Lebberston Member and the Scarborough Formation contain occasional dinoflagellates and marine algae, which reflect the marine environments of these units.

DISCUSSION

Short-term vs long-term variation in sporomorph assemblages

Comparing variation in sporomorph and palynofacies assemblages with lithology and more generally with time
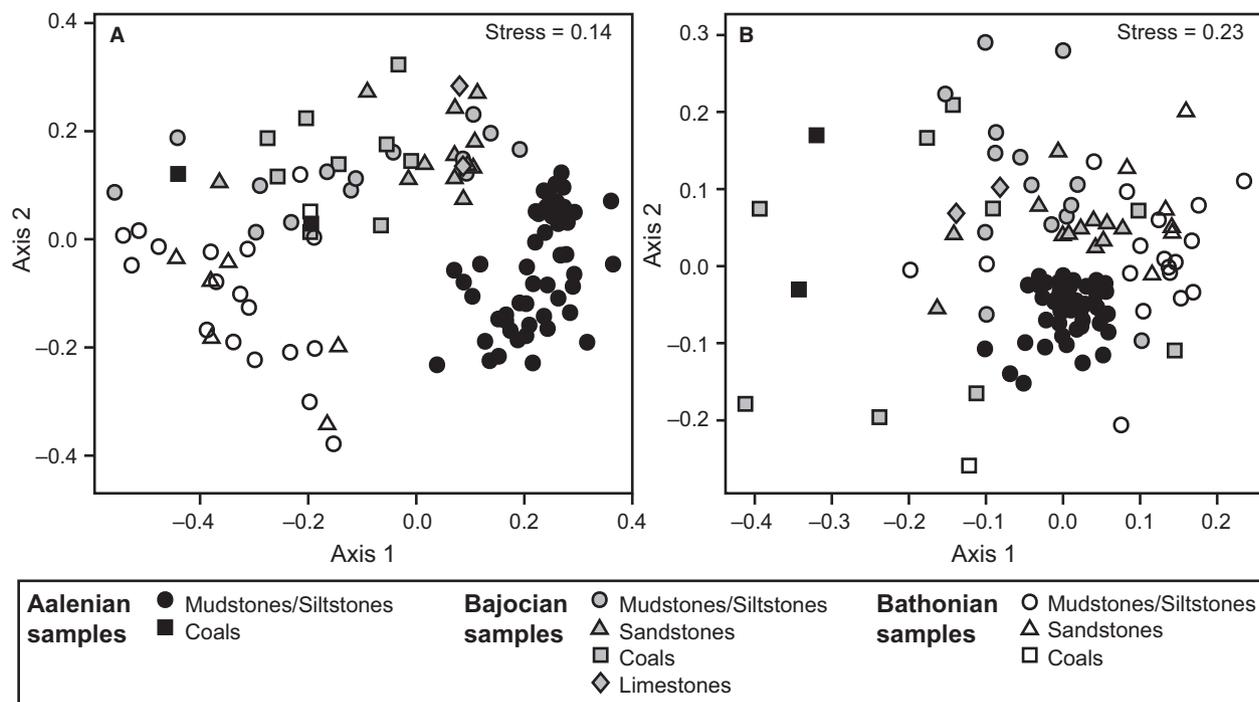
FIG. 12. Non-metric multidimensional scaling plots of sporomorph data. A, relative abundance data. B, presence–absence data.

can help to extract information on respective short-term and long-term changes in vegetation and depositional environments. Such comparisons can assist to determine whether temporal variation in these fossil assemblages represents 'true' variation in parent vegetation, or is simply the result of variable taphonomic processes through time.

Abundance/richness plots and ordinations (Figs 8–13) demonstrate that variation between sporomorph and palynofacies assemblages correlates with lithology/depositional setting within individual sections. This is particularly apparent at Hasty Bank, where assemblage composition differs considerably between the lower and upper parts of the section, between which there is a change in depositional setting. Thus, a change in parent vegetation and/or taphonomic processes, which shape sporomorph assemblages, is not particularly surprising (Slater and Wellman 2015). Furthermore, within individual sections there are often considerable abundance variations of taxa from samples that are stratigraphically very close to one another. Hence, relatively short-term depositional change within individual sections has a measurable impact on the following: (1) parent vegetation and resultant sporomorph assemblages; and/or (2) preferential preservation of certain sporomorphs due to taphonomic processes.

Within individual sections (e.g. section 5) samples taken from similar lithologies generally have similar palynofloral compositions. Broadly speaking, within individual

sections, overbank deposits are characteristically composed of rich palynofloras with abundant conifer pollen, channel sediments are routinely composed of rich assemblages with abundant ferns and conifers, and coals and other confined deposits (e.g. abandoned channels) are typically composed of abundant fern assemblages with very low overall richness levels. This correlation between sporomorph assemblages and lithology/depositional setting is due to a combination of: (1) similar vegetation; and (2) similar depositional/taphonomic processes occurring within these parallel environments. Specifically, the high overall richness levels and abundant conifer pollen in floodplain samples is probably a result of the large source areas supplying such deposits (Behrensmeyer and Kidwell 1985; Behrensmeyer et al. 2000), with multiple river channels potentially feeding hinterland taxa into these settings, thus increasing conifer abundances and richness. The relatively rich sporomorph assemblages recognized within channel sediments are, similarly to floodplain deposits but to a lesser extent, the result of relatively large source areas. Multiple tributaries would have potentially flowed into these channels, hence source area size is increased and abundances of coniferous hinterland taxa and overall richness are increased alike. The high abundances of ferns, low abundances of conifers and low richness levels within coal and abandoned channel deposits are likely a result of the confined source areas that supplied these deposits. Hence, coals and abandoned channel deposits sampled within this study are more
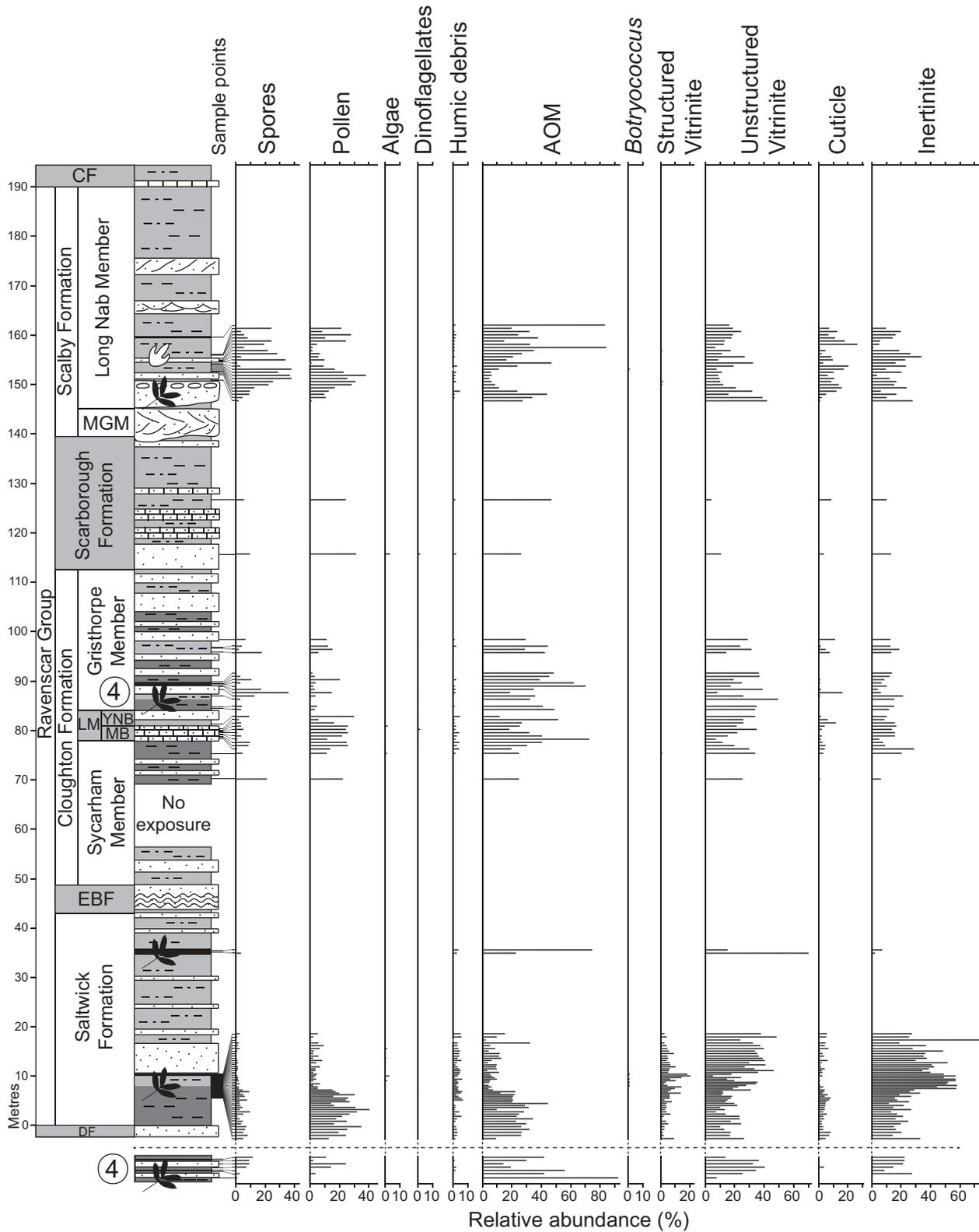
FIG. 13. Relative abundances of palynofacies categories. Shaded text regions in the log represent marine units; CF, Cornbrash Formation; DF, Dogger Formation; EBF, Eller Beck Formation; LM, Lebberston Member; MB, Millepore Bed; MGM, Moor Grit Member; YNB, Yons Nab Beds. In the composite log '4' refers to the stratigraphic position of section 4.

representative of the parent vegetation close to the site of deposition compared to most other lithologies/depositional environments, which are generally more representative of the regional flora. The results here indicate that with decreased source area size, there is a decrease in the ratio of coniferous pollen compared to other sporomorphs. This suggests that abundant coniferous parent vegetation did not occupy the interior of the sedimentary basin, but instead, conifers were typical of extrabasinal/hinterland environments, whereas coal and abandoned channel samples demonstrate that primarily ferns dominated the interior of the basin.

Chaloner and Muir (1968) compared Jurassic sporomorph assemblages from Yorkshire from different lithologies and demonstrated that, when sporomorphs were grouped morphologically, assemblages were compositionally more similar to each other according to their respective lithologies than they were according to their sampled stratigraphic position. This relationship was attributed to changes in base level, which altered the relative areas of different communities and their proximity to sampling sites (Chaloner 1968; Chaloner and Muir 1968). Similar results are apparent in this study. However, ordination of samples (Fig. 12) based on individual taxa (i.e. where sporomorphs have not been grouped as in Chaloner and Muir (1968)) reveals that samples cluster primarily according to their stratigraphic position and secondarily according to their lithology; thus, samples appear more similar to one another in terms of their age than their lithology/depositional setting. Therefore, as postulated by Chaloner and Muir (1968), long-term changes in sporomorph assemblages are seemingly more apparent when taxa are analysed individually and are probably more important than short-term assemblage variations through individual sections (e.g. Hasty Bank). Coal samples are an exception to this rule, as sporomorph assemblages from coals sampled here are more similar to each other according to their lithology than they are according to their sampled stratigraphic position, presumably due to their very localized catchment areas. The pattern described by Chaloner and Muir (1968) was more extreme in their study because the lithologies/depositional environments sampled were more varied than the environments sampled in this study. For example, they analysed samples ranging from marine black shales to terrestrial coals; thus, there was high compositional variation between these highly different depositional environments even when samples were synchronous. The depositional environments sampled in this study are less varied, thus helping to explain why, with the exception of coals, variation between samples appears to be primarily stratigraphic and secondarily lithological/depositional.

Figures 8–13 reveal a dynamic long-term palynofloral history for the Ravenscar Group in which fern spores gradually become dominant over conifer pollen from the Aalenian into the Bathonian. Lycophytes and pteridosperms/conifers become markedly more abundant in the Bathonian, and conversely monosulcate producers and sphenophytes become considerably less abundant in the Bajocian and Bathonian. Although short-term taphonomic controls are highly important, such controls are superimposed on long-term variations in sporomorph assemblages, which are more apparent when taxa are analysed individually. Long-term variations are considered to be representative of changes in depositional environments through time, which influence depositional taphonomic processes and parent vegetation, thus giving rise to temporal variations in sporomorph assemblages.

Biases in the sporomorph record

Extracting true changes in parent vegetation through time using the sporomorph record is often problematic, as ecological and taphonomic biases can dramatically affect the composition of assemblages (e.g. Chaloner and Muir 1968).

Perhaps the most important biological factor in shaping assemblage composition is the variation in spore/pollen production levels between plant groups as a result of different reproductive strategies. For example, sporomorph production in wholly wind-dispersed taxa, such as the conifers and ferns, is typically very high; thus, such plant groups are overrepresented compared to reproductively specialized taxa (e.g. Mander et al. 2010). Therefore, abundances of sporomorph plant groups almost certainly do not accurately reflect the abundances of parent plant groups within the palaeofloristic community. However, all factors being equal, temporal changes in sporomorph abundances often do fairly reflect regional-scale abundance change within a particular plant group, as sporomorph production levels presumably do not vary greatly within plant groups through time.

The proximity of parent plants in relation to their depositional setting plays an important role in governing assemblage composition. An example of this is visible in this study; sample P4 contains exceptionally high abundances of the lycophyte spore *Densoisporites velatus*, which is typically rare in all other samples. This sample presumably originates from a deposit with a confined source area, which was occupied by the lycophyte parent plant. Hence, sample P4 almost certainly does not accurately reflect the regional flora, but provides insight into the parent vegetation close to the site of deposition. Determining information on the relative proximity of parent plants to their depositional setting is potentially possible regarding some of the reproductively specialized taxa such as the cycads. Kono and Tobe (2007) demon-

strated that the pollen of the modern cycad, *Cycas revoluta*, occurs only in abundance within close proximity to the parent plant. Thus, if Jurassic equivalents share this characteristic, deposits that are abundant in cycad pollen potentially formed within close proximity to the cycad parent plants.

The differential physical durability of taxa plays an important role in influencing assemblage composition. For example, many fern spores possess relatively thick spore walls (e.g. *Deltoidospora*) and are thus reasonably resistant to taphonomic processes such as transportation and corrosion. Conversely, some spores, such as *C. mesozoica*, possess a thin spore wall and contain little sporopollenin (Traverse 2007; Grauvogel-Stamm and Lugardon 2009) and are resultantly comparatively underrepresented.

A further problem with the sporomorph record is that many parent plants produce sporomorph taxa that appear superficially indistinguishable from one another, particularly when using only light microscopy (e.g. Mander and Punyasena 2014). This is particularly apparent within the Jurassic cycads and ginkgos, which typically produce simple, monosulcate pollen that display no obvious distinguishing features under light microscopy (e.g. Frederiksen 1980). Thus, when using sporomorphs to make palaeofloristic reconstructions, it is sensible to group sporomorphs at a relatively high taxonomic level, preferably at family level or higher.

Depositional environment is a fundamental factor controlling the composition of parent vegetation and resultant sporomorph assemblages. Additionally, different depositional environments often display considerable variation regarding the geographical catchment areas that supply deposits. This relationship is particularly apparent regarding the low richness levels visible in a number of coal samples. The associated rootlet beds present directly below the coals at Hayburn Wyke and Cloughton Wyke suggest that these deposits formed *in situ*. These coals potentially represent small, confined swamps that have formed above a soil horizon. All coals sampled here are considerably less extensive than the prominent drifted coal seam present at Brora, Scotland, which has yielded assemblages of abundant and diverse palynomorphs (e.g. Couper 1958; Hughes and Couper 1958; Lam and Porter 1977; Riding 2005). Presumably, the coals sampled here were supplied by relatively small geographical catchment areas; thus, input into these coal-forming environments is reduced and sporomorph richness is reduced accordingly. Conversely, the high richness of Aalenian samples at Hasty Bank reflects the depositional environments there; samples originate from a probable floodplain and fluvial channel environment (Slater and Wellman 2015). Such depositional environments were potentially supplied by very large geographical catchment areas compared to con-fined coal-forming swamps, and resultantly richness is considerably higher in these deposits.

Variable transportation processes and distances also influence sporomorph assemblage composition. Spores and pollen can be considered as sedimentary particles during transport and depositional processes. Hence, differences in factors such as particle size, shape and density influence whether certain sporomorphs are preserved in a particular depositional setting. Evidence for these variable processes is visible here; samples from the marine Lebberston Member contain low numbers of fern spores and high numbers of conifer pollen; this pattern is mirrored in the overlying non-marine Gristhorpe Member. This almost certainly does not reflect genuine parent vegetation change, but is the result of variable taphonomic processes between these units comparable to the 'Neves effect' (Chaloner and Muir 1968). Specifically, the reduced clastic input/fluvial connection in the Lebberston Member means that 'light' conifer pollen is more likely to reach these environments via water and air transport compared to 'heavy' fern spores that predominantly require fluvial action to be transported into the marine system. Similar patterns are visible in the Long Nab Member; the high abundances of cuticle and spores relative to pollen in the Long Nab Member potentially indicates less extensive and/or lower energy transportation distances and processes for Bathonian samples. Fragile cuticle is likely to be destroyed during extensive transportation (Cross *et al.* 1966; Muller 1959), and a high percentage of spores compared to pollen often signifies that assemblages are derived from a close proximity to parent vegetation (e.g. Habib 1982).

Spatial variations in depositional environments can have large consequences on sporomorph assemblages (e.g. Chaloner and Muir 1968). Samples from section 4 and the lower part of the Gristhorpe Member from section 3 are roughly synchronous; these samples display high compositional similarity suggesting little spatial floral variation between these localities. Minimal variation was also noticed between synchronous samples from Burniston Bay. The similar sporomorph assemblages between these synchronous deposits with slightly different depositional settings suggest that temporal variations in assemblages are representative of potentially substantial changes in depositional processes and/or accompanying parent vegetation and indicate that spatial variations in local floras of the examples discussed are relatively minor.

Comparison with the plant mega/mesofossil record

Changes in composition between plant megafossil assemblages through the Ravenscar Group are generally well

documented following extensive collection and description of specimens from numerous palaeobotanical studies over the past century (see Van Konijnenburg-Van Cittert and Morgans 1999). Harris (1952) discussed ranges of plant megafossil taxa through the Middle Jurassic of Yorkshire. He observed that, unlike underlying and overlying strata, the plant megafossil assemblages of the Cloughton Formation were dominated by conifer cuticle and that some ginkophytes and cycadophytes were absent. The spore and pollen record in this study agrees with these observations in that samples from the Cloughton Formation are dominated by conifer pollen and simple monosulcate pollen is markedly less abundant compared to underlying Aalenian samples and moderately less abundant than overlying Bathonian samples (Fig. 9). Hence, both sporomorph and plant megafossil records suggest that cycad and ginkgo parent vegetation was less abundant in the Bajocian compared to the Aalenian and Bathonian.

Van Konijnenburg-Van Cittert and Morgans (1999) demonstrated that the plant megafossil *Equisetum* is markedly more abundant within the Aalenian plant beds of the Ravenscar Group. The sporomorph record agrees with this observation; *Calamospora* is also more abundant within the Aalenian samples from Hasty Bank compared to Bajocian and Bathonian samples. As both fossil assemblages record the same temporal abundance patterns this potentially reflects a 'true' vegetation change and suggests that *Equisetum* was more abundant in the Aalenian.

Slater and Wellman (2015) compared plant megafossil (Spicer and Hill 1979) and dispersed sporomorph assemblages through the Hasty Bank plant bed and recognized notable discrepancies between assemblages regarding the nature of parent vegetation. Specifically, conifers and ferns were underrepresented in plant megafossil assemblages, bryophytes and lycopsids were represented only in sporomorph assemblages, and sphenophytes, pteridosperms, Caytoniales, Cycadales, Ginkgoales and Bennettitales were comparatively underrepresented in sporomorph assemblages. The major causes for these discrepancies were attributed to a multitude of biological and taphonomic biases including the following: variation in sporomorph production levels between parent plants, depositional environment, variation in sporomorph and parent plant durability and the proximity of parent plants in relation to the site of deposition. Similar results were identified from Triassic–Jurassic sequences of East Greenland (Mander *et al.* 2010) and from Lower Jurassic deposits of Odrowąż, central Poland (Ziaja 2006), suggesting that the taphonomic/ecological causes for the discrepancies between the sporomorph and plant megafossil assemblages occur across a range of different depositional environments and localities.

Comparison with climatic changes and regional-scale vegetation

Diverse parent vegetation and favourable taphonomic conditions mean that the total diversity of the Yorkshire Jurassic flora is high. Furthermore, excellent sedimentary exposure and extensive investigation into these deposits means that this diversity is well known, particularly when compared to other contemporaneous regional deposits. Coeval deposits from Gloucestershire and Oxfordshire are generally less diverse in terms of their sporomorph and megafossil assemblages (e.g. Riding 1983; Cleal and Rees 2003; Srivastava 2011) due to these taphonomic and collection biases. Nonetheless, despite these factors floral compositions do appear to display some consistencies with regional deposits (e.g. Boulter and Windle 1993).

Determining the causes of vegetation change in the fossil record is frequently problematic as there are numerous possible variables that can influence floral communities through time. Such variables include climatic, ecological, geographical and depositional factors. Chaloner (1968) and Chaloner and Muir (1968) postulated that changing sporomorph assemblages through the Jurassic of Yorkshire could be the result of changing base level, under a constant climate; however, they emphasize that climatic changes could also be involved. More recent climatic interpretations through the Middle Jurassic of Yorkshire suggest multiple changes through these sequences. Based on fossil wood material collected through the Ravenscar Group, Hesselbo *et al.* (2003) recorded a negative δ^{13}C isotope excursion at the Aalenian–Bajocian boundary, across which the dominant preservation mode of fossil wood changed from charcoal to coal, suggesting a shift to a more continuously humid climate in the early Bajocian. Their findings were also indicative of a seasonally arid environment in the middle Bajocian marked by an increase in charcoal preservation mode. Hesselbo *et al.* (2003) stated that the megafloral record, based on findings by Harris (1961, 1964, 1969, 1979) and Harris *et al.* (1974), appeared to contradict the C-isotope results in that vegetation change apparently suggested a change from 'wetter' to 'drier' environments with a decrease in diversity from the Aalenian into the early Bajocian.

Boulter and Windle (1993) used dispersed sporomorph data in combination with megafloral records from Yorkshire and across the UK to reconstruct Middle Jurassic vegetation. Their findings suggested three distinct floral communities through the Middle Jurassic: (1) 'Mesozoic gymnosperms' in the Aalenian; (2) 'fern prairies' in the middle Bathonian; and (3) 'conifer forests' in the late Bathonian. Both Bathonian floras were however dominated by conifer pollen and these two communities were considerably more similar to each other than they were compared to Aalenian palynofloras. The three

communities described by Boulter and Windle (1993) are analogous to the vegetation reconstructions in this study. Specifically, 'Mesozoic gymnosperm' communities are highly similar in composition to the Aalenian Hasty Bank samples in this study and the Bathonian 'fern prairies' and 'conifer forests' from Oxfordshire and Northamptonshire are similar to the palynofloras of the Bathonian Long Nab Member in this study. This suggests high floral compositional similarity between these localities and/or similar taphonomic processes were acting on assemblages to preserve similar fossil records. Boulter and Windle (1993) suggested that the change from 'Mesozoic gymnosperm' communities in the Aalenian to conifer dominated palynofloras in the Bajocian and Bathonian could be indicative of the following: (1) conifers occupying niches left by other plants; and/or (2) increased aridity in the Bajocian and Bathonian. Equally, the 'Mesozoic gymnosperm' communities of the Aalenian are potentially suggestive of more humid conditions compared to the Bathonian (Boulter and Windle 1993).

Based on sporomorph assemblages from multiple localities across Europe (including the Jurassic of Yorkshire) and Australia, Hubbard and Boulter (1997) used groupings of climate indicative taxa to reconstruct climatic variation through parts of the Mesozoic. Their findings suggested overall temperatures decreased slightly near to the Aalenian–Bajocian boundary, temperatures then rose gradually towards the Bathonian–Callovian boundary. Hubbard and Boulter (1997) demonstrated that sporomorph groupings at Hasty Bank were dominated by cold adapted taxa, indicating relatively cold climatic conditions in the Aalenian. Bajocian assemblages from Cloughton Wyke and Yons Nab were codominated by cold–intermediate climatically adapted taxa and Bathonian assemblages from Scalby Ness and Gristhorpe were composed of a mixture of warm, intermediate and cold adapted taxa, thus suggesting a rise in temperatures from the Aalenian to the Bathonian.

Sporomorph evidence in this study concurs with previous megafloral (Harris 1961, 1964, 1969, 1979; Harris *et al.* 1974) and sporomorph investigations (Boulter and Windle 1993; Hubbard and Boulter 1997) from the Middle Jurassic of Yorkshire. Specifically, the megafloral record agrees with the sporomorph record in that diversity here appears to decrease from the Aalenian into the Bajocian and floral abundances shift from a heterogeneous mixture of conifers, ferns, monosulcate producers, sphenophytes and Caytoniales to a more homogeneous assemblage, codominated by conifers and ferns. Similarly to previous sporomorph investigations (Boulter and Windle 1993), assemblages here display a marked decrease in monosulcate producers at the end of the Aalenian.

Cleal and Rees (2003) investigated the Middle Jurassic fossil flora of Stonesfield, Oxfordshire. This is considered to represent mostly coastal vegetation with abundant Cheirolepidiaceae. The marine depositional setting at Stonesfield undoubtedly influences the taphonomy of the assemblages; despite this, terrestrial vegetation appears to be somewhat different to that of the Yorkshire Jurassic. Floras of Stonesfield are less diverse and possess no horsetails, and ferns and Ginkgoalean foliage are poorly represented. Cleal and Rees (2003) suggest that the Stonesfield flora represents a seasonally dry climate; whilst Yorkshire and the Araucariaceae dominated floras from the Isle of Skye (Bateman *et al.* 2000; Cleal *et al.* 2001) represent warm-temperate climatic conditions.

Although climatic interpretations display some general consistencies, it is difficult to state with certainty whether the apparent changes in vegetation recorded in this study are definitely related to climatic events, as there are numerous factors that could cause such changes to occur. The majority of temporal changes seen in sporomorph assemblages here are interpreted to be due to long-term changes in depositional environments through the Ravenscar Group which result in differences in depositional taphonomic processes and parent vegetation through time. For example, the variation in assemblages seen between non-marine and marine units, particularly regarding the ratios fern spores to conifer pollen is greatly affected by changes in depositional taphonomy. However, changes in the proximity of the coastline to the basin interior (i.e. the palaeogeographical position of the coastline) will also influence parent vegetation, as numerous environmental factors (e.g. salinity, water supply and ground disturbance) will change with distance from the shoreline.

Emerging reconstruction

Despite the numerous biases within the sporomorph record, it is clear that this fossil data can be useful in the assessment of palaeovegetation change through time, particularly when depositional context is taken into account. Integrating the sporomorph record with multiple fossil assemblages (e.g. plant megafossils) and geochemical proxies (e.g. C-isotope data) is an important task in refining palaeoenvironmental reconstructions. The emerging picture from this study compliments previous palaeoenvironmental (e.g. Alexander 1989) and palaeogeographical (e.g. Rawson and Wright 2000) reconstructions for the Cleveland Basin. The general consensus in the literature is indicative of a lowland coastal plain basin interior that was periodically flooded by seawater (e.g. Ielpi and Ghinassi 2014), surrounded by upland environments (Rawson and Wright 2000). This study suggests the basin interior was occupied mostly by low-standing, lush species and the extrabasinal vegetation was dominated by

coniferous taxa. Interestingly, samples from the dinosaur footprint bed at Burniston Bay (JP1/7 and JP2/8) contained highly abundant fern spores (*D. minor* and *D. harrisii*), with low abundances of conifer pollen and diverse lycophyte assemblages. The co-occurrence of abundant footprints (e.g. Whyte *et al.* 2007) with low-standing, relatively lush vegetation within the basin interior is indirect evidence to suggest herbivorous dinosaurs were visiting this area to feed.

CONCLUSIONS

The Aalenian, Bajocian and Bathonian stages possess relatively distinct sporomorph assemblages, which potentially reflect a dynamic history for the nature of parent vegetation through the Middle Jurassic of Yorkshire. Specifically, Aalenian floras were composed of a heterogeneous mixture of conifers (conifers dominate), ferns, monosulcate producers, sphenophytes and Caytoniales. Bajocian floras were more homogeneous in composition than Aalenian and Bathonian counterparts and were codominated by conifers (conifers dominate) and ferns, with low abundances of all other plant groups. Bathonian communities were highly rich and composed of abundant ferns (ferns dominate), conifers, lycophytes, pteridosperms/conifers and Caytoniales. Vegetation reconstructions from this study combined with previous palaeogeographical reconstructions for the Cleveland Basin (e.g. Rawson and Wright 2000) suggest that the basin interior was occupied by low-standing, lush species and extrabasinal vegetation was dominated by coniferous taxa. Long-term changes in composition are probably a result of depositional and/or climatic changes, which altered depositional taphonomic processes and parent vegetation. Comparisons of the dispersed sporomorph and plant megafossil records through the Ravenscar Group indicate that both fossil assemblages reflect different aspects of the parent vegetation due to a multitude of taphonomic and ecological biases. Such biases include variation in spore/pollen production levels between plant groups, differences in transportation and depositional processes, variation in spore/pollen and parent plant durability and the proximity of parent plants in relation to the site of deposition.

DATA ARCHIVING STATEMENT

The following data for this study are available in the Dryad Digital Repository (http://dx.doi.org/10.5061/dryad.cc0m7):
Appendix S1. Sample processing details.
Appendix S2. Raw data set of all sporomorph counts. Sample heights provided.
Appendix S3. Raw data set of all palynofacies counts. Sample heights provided.
Appendix S4. Botanical affinities of sporomorphs. Adapted from Slater and Wellman (2015).
Appendix S5. Non-metric multidimensional scaling axis scores of samples using relative abundance data (refers to Figure 12A).
Appendix S6. Non-metric multidimensional scaling axis scores of samples using presence–absence data (refers to Figure 12B).

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